

Simone Hofstetter · Willy Tinner ·
Verushka Valsecchi · Gabriele Carraro ·
Marco Conedera

Lateglacial and Holocene vegetation history in the Insubrian Southern Alps—New indications from a small-scale site

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Abstract Fundamental uncertainties exist in the study region about the former lowland vegetation at local scales. All existing palaeoecological results are derived from sediments of medium- to large-sized sites (8–5000 ha), which are thought to record mainly regional vegetation in their pollen content. Therefore the very small mire at Balladrum (0.05 ha) was analysed for pollen, plant-macrofossils, and charcoal and the results compared with those of previous studies in the same region. Common regional signals were detected, but also new insights for the tree species *Pinus cembra* (L.), *Abies alba* (Mill.) and *Castanea sativa* (Mill.). Our palaeobotanical data reveal the local dominance of the timberline species *P. cembra* during the Lateglacial (16500–14250 cal B.P.) at low-altitudes. For *A. alba* an early presence in the area is suggested by pollen data, corroborating previous high-altitudinal studies indicating the presence of glacial refugia in the region. Occasional findings of *C. sativa* pollen throughout the Holocene may indicate the local but very rare presence of this species in the Insubrian Southern Alps, in contrast to the conventional

opinion that *C. sativa* was introduced during the Roman Period. Altogether the results confirm the need of multiproxy palaeobotanical records from basins of variable size to assess the past composition of vegetation more accurately.

Keywords Vegetation history · Southern Alps · Small versus large basins · *Pinus cembra* · *Abies alba* · *Castanea sativa*

Introduction

For understanding the dynamics of the present vegetation it is important to know the vegetation history as precisely as possible. In particular, vegetation-history information may help to assess the natural potential vegetation (e.g., Tinner et al. 1999). In areas where severe cultural disturbance changed the natural species composition, this is essential for forest management (DIONE SA unpubl.; Frehner et al. 2005). In this regard, palaeobotanical investigations represent a very useful tool for reconstructing past species composition and for measuring the anthropogenic influence on ecosystems. Unfortunately, in the Insubrian Southern Alps fundamental uncertainties exist about the former lowland vegetation at local scales. All existing modern palaeoecological results are derived from sediments of medium to large-sized sites (8–5000 ha). They reflect mainly regional vegetation within a radius of several hundred meters to kilometres around the sites. More local pollen signals can only be detected by investigations at small-scale sites (Jacobson and Bradshaw 1981; Sugita 1994; Calcote 1995; Lynch 1996; Broström et al. 1998; Jackson and Kearsley 1998; Sugita et al. 1999; Parshall and Calcote 2001).

In this paper we report for the first time the results of a palaeoecological investigation on a small-scale lowland site (<0.1 ha) in the Insubrian Southern Alps providing a complete Holocene and Lateglacial biostratigraphy. To improve spatial resolution analyses of pollen and microscopic charcoal were combined with plant macrofossils (Birks and Birks 2000; Birks 2003) and macroscopic charcoal

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S. Hofstetter (✉) · W. Tinner · V. Valsecchi
University of Bern, Institute of Plant Sciences,
Altenbergrain 21,
CH-3013 Bern
e-mail: simone.hofstetter@ips.unibe.ch

V. Valsecchi
University of Milan, Earth Sciences Department “A. Desio”,
Via Mangiagalli 34,
I-20133 Milano

G. Carraro
DIONE SA, Environmental Consulting and Forestal
Engineering,
Lungolago Motta 8,
CH-6600 Locarno

M. Conedera
Swiss Federal Institute for Forest, Snow and Landscape
Research, WSL,
Sottostazione Sud delle Alpi, PO Box 57 CH-6504
Bellinzona-Ravecchia

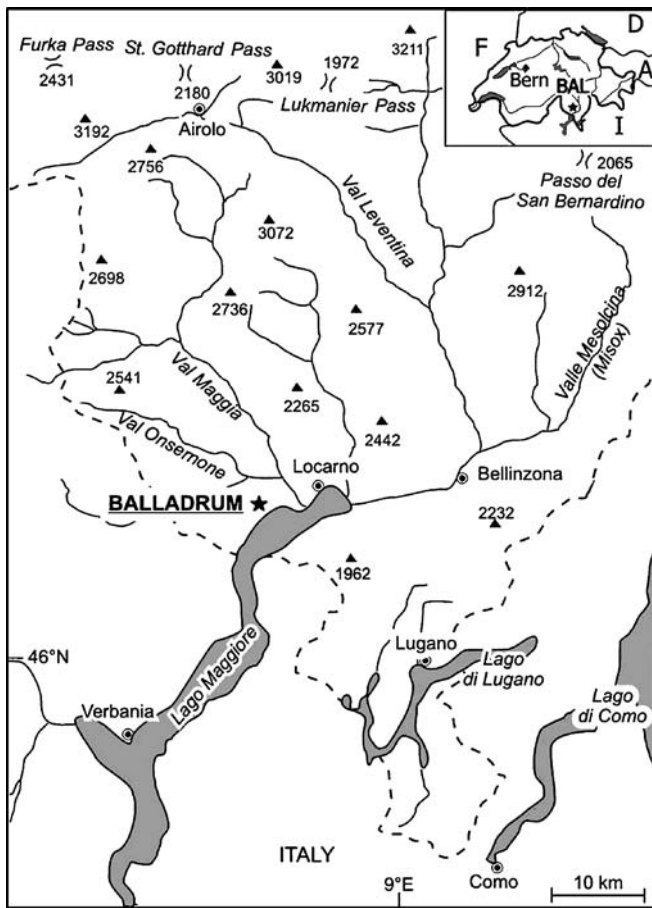


Fig. 1 Map of southern Switzerland, showing the location of the study site Balladrum at the northern border of Lago Maggiore

(Clark 1995; Whitlock and Larsen 2001). The main aims of the presented investigation were (1) to reconstruct local vegetation and fire history for a small-scale site in the Insubrian lowlands and (2) to discuss potential differences between this and previous studies in the region.

Study area and study site

The area of interest is located in the central part of the Insubrian southern Alps (Fig. 1), between Lago Maggiore and Lago di Como. This region has a special vegetation history in Europe. The lowlands were once covered by species-rich mixed forests. *Abies alba* was important and many deciduous trees were present, such as *Tilia*, *Ulmus*, *Fraxinus*, *Quercus*, and *Acer*. Starting in the Neolithic, these forests were strongly disturbed and landscape was opened. At the beginning of the Roman Times the idea of systematically cultivating chestnut was promoted and therefore *Castanea sativa* favoured (Conedera et al. 2004a). Recently the Insubrian region has been subject to significant ecological changes. Evergreen broad-leaved species are expanding, probably in response to increasing winter temperatures (Walther et al. 2002) and decreasing land-use intensity (Kloetzli et al. 1996; Carraro et al. 1999; Conedera

et al. 1999). For several millennia people altered the forest composition, with fire as the most important tool (Tinner et al. 1999). In this way important forest elements such as *Abies alba* were excluded. Therefore it has been hypothesised that unoccupied ecological niches were generated, favouring the invasion of evergreen species (Gianoni et al. 1988; Grund et al. 2004). In addition, abandoned chestnut groves began to be invaded by other thermophilous deciduous tree species, due to the end of active cultivation (Conedera et al. 2000, 2001, 2004b).

The studied mire (390 m a.s.l., 8° 45' E and 46° 1' N, Fig. 2) is situated in southern Switzerland (Fig. 1) 0.5 km north of Lago Maggiore at the foot of a hill called Balladrum (483 m a.s.l.). The present surface area is 500 m², overgrown by *Carex acutiformis*. The hummocky landscape around it was formed by the Ticino glacier

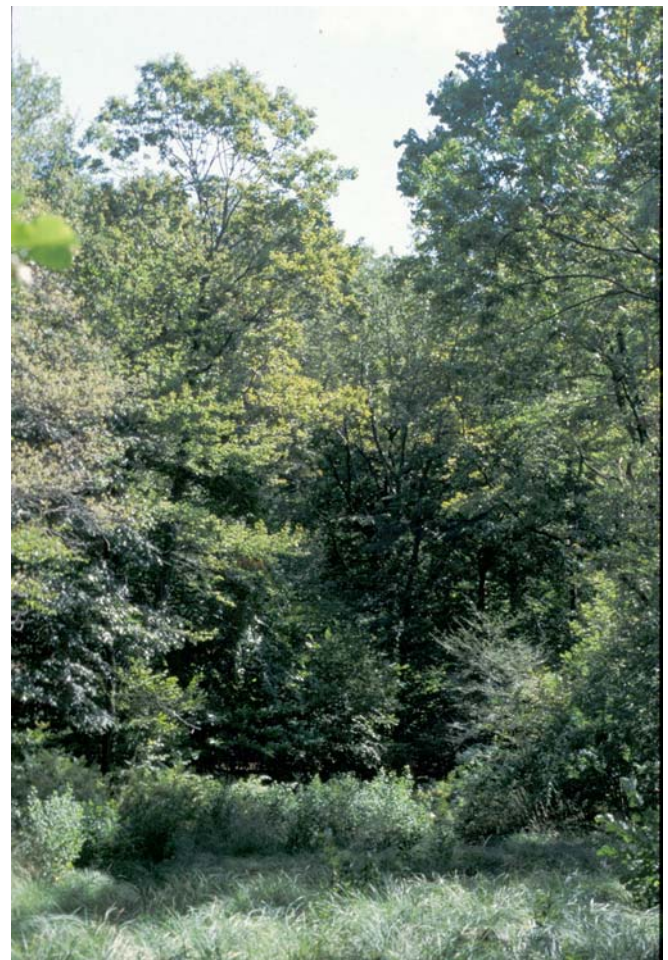


Fig. 2 Picture of the mire at Balladrum, taken from its center in eastern direction. Surface area is 0.05 ha (ca. 10 m × 50 m) and overgrown by *Carex acutiformis*. *Carex gracilis* and *C. rostrata* are present in small quantities. Trees next to the mire are ca. 20 m high and the vegetation is dominated by *Quercus robur* and *Q. robur* × *Q. petraea*, while *Castanea sativa* and *Tilia cordata* are scattered. *Alnus glutinosa* and *Frangula alnus* are locally dominant around the mire. One side of the mire is limited by a steep rocky slope (on the right), the other by a hummock. One of the few relictic *Abies alba* lowland stands of the Southern Alps is growing at 500 m distance. Photo: W.O. van der Knaap

(Hantke 1983). It includes stony slopes and many small wetlands in between the roches moutonnées and drumlins. The catchment is principally formed by metamorphic rocks (Ehrensberger 1984; Labhart 1995). Summers are very humid, winters relatively dry and warm. At the northern border of Lago Maggiore winter is extremely mild (January mean temperatures 1980–1995 were 2.5 °C; Maggini and Spinedi 1996), this special climate type is called “hyperinsubric” (Steiger 1994). Already Zoller (1960) stated that such favourable conditions are only found again south of the Po Plain. The vegetation around the study site is dominated by *Castanea sativa*. Common in the open forests is *Cistus salvifolius*, an evergreen shrub typical for the Mediterranean region. One of the very rare surviving lowland stands of *Abies alba* grows on quite acid soils 500 m distant, associated with *Castanea sativa*, *Fraxinus excelsior*, *Tilia cordata*, *Trachycarpus fortunei*, *Corylus avellana*, and *Hedera helix*.

Material and methods

Coring, sediments and dating

The sediment was taken with a Streif modified Livingstone piston corer (Merkt and Streif 1970). Two parallel cores were recovered 50 cm apart. Core 1 (BAL1) is 227 cm long, core 2 (BAL2) 193 cm. The sediment of BAL1 was watery from 145 cm upwards, and therefore only the lower part of this core was analysed. Terrestrial plant-macrofossils were dated with Accelerator Mass Spectrometry (AMS) at the Poznan Radiocarbon Laboratory (Poland), two from BAL1 and six from BAL2. The ^{14}C dates were calibrated by the program CALIB 4.3 (Stuiver and Reimer 1998).

Analysis of pollen, plant-macrofossils and charcoal

Standard techniques including treatment with HCL, KOH, HF, and acetolysis (Moore et al. 1991) were used for preparation of sediment samples of 1 cm³ volume. *Lycopodium* tablets were added for calculation of pollen concentrations (Stockmarr 1971). The prepared samples were stored in fluid glycerine. For each sample minimal 600 terrestrial pollen grains were counted and identified with use of the

reference collection of the Institute of Plant Sciences at the University of Bern and pollen keys and atlases (Moore et al. 1991; Reille 1992; Beug 2004). TILIA and TILIA-GRAPH programs (Grimm 1992) were used to construct the diagrams. To determine local pollen assemblages zones (LPAZ) numerical zonation was carried out by optimal sum of squares partition (Birks and Gordon 1985). The number of statistically significant splits was determined with the broken-stick model (Bennett 1996). Statistically non-significant local pollen assemblage subzones were added.

Plant-macrofossils were analysed according to standard procedures (Birks 2001). In both cores a sediment volume of 22 cm³ was taken at 4-cm intervals. The sediment was washed with water through a sieve with 0.2 mm mesh. The residue after sieving was frozen in distilled water for preservation. The examination was carried out with the help of a seed collection of the Institute of Plant Sciences at the University of Bern, recent plant material and keys (e.g., Schoch et al. 1988; Tobolski 1992). Remains of *Pinus sylvestris* type could not be identified to species level (Struzkova 2002) due to bad preservation. The concentration-diagrams were made with TILIA and TILIAGRAPH (Grimm 1992). For better comparison, the zones determined by pollen analysis were transferred to the macrofossil diagrams.

Microscopic charcoal particles longer than 10 µm were counted in the pollen slides. Particle concentrations (charcoal particles cm⁻³) were estimated by using the same approach as for pollen (Tinner and Hu 2003; Finsinger and Tinner 2005), and influx (charcoal particles cm⁻² yr⁻¹) was then calculated. Charcoal in pollen slides can be used to reconstruct regional fires (MacDonald et al. 1991; Tinner et al. 1998; Whitlock and Larsen 2001). We estimated also the area (mm² 22 cm⁻³) of macroscopic charcoal particles larger than 200 µm, which are mostly delivered to the sediment from local sources (Clark et al. 1989; Tinner et al. 1998; Whitlock and Larsen 2001).

Results

Chronology

The ^{14}C ages are presented in Table 1. The depth-age model relies on calibrated ages (cal B.P., Fig. 3) and was built by linear interpolation of the dates. The calibrated ages of

Table 1 AMS radiocarbon dates of Balladrum, core 1 (BAL1) and core 2 (BAL2)

Lab code	Depth (cm)	^{14}C Age (uncal B.P.)	Age (cal B.P.)	2σ range (cal B.P.)
Core 1				
Poz-2039	175.5–176.5	11140±60	13142	13369–12893
Poz-2040	199.5–200.5	3100±100	15749	16255–14664
Core 2				
Poz-2041	74.5–75.5	2470±35	2613	2734–2356
Poz-6498	105.5–109.5	3215±30	3425	3473–3362
Poz-6500	113.5–117.5	4160±35	4720	4830–4533
Poz-2042	136.5–137.5	3185±35*	3387*	3470–3349*
Poz-6501	145.5–149.5	9340±50	10557	10688–10293
Poz-2044	180.5–182.5	11410±80	13416	13799–13052

*Date regarded as unreliable and not used in construction of chronology

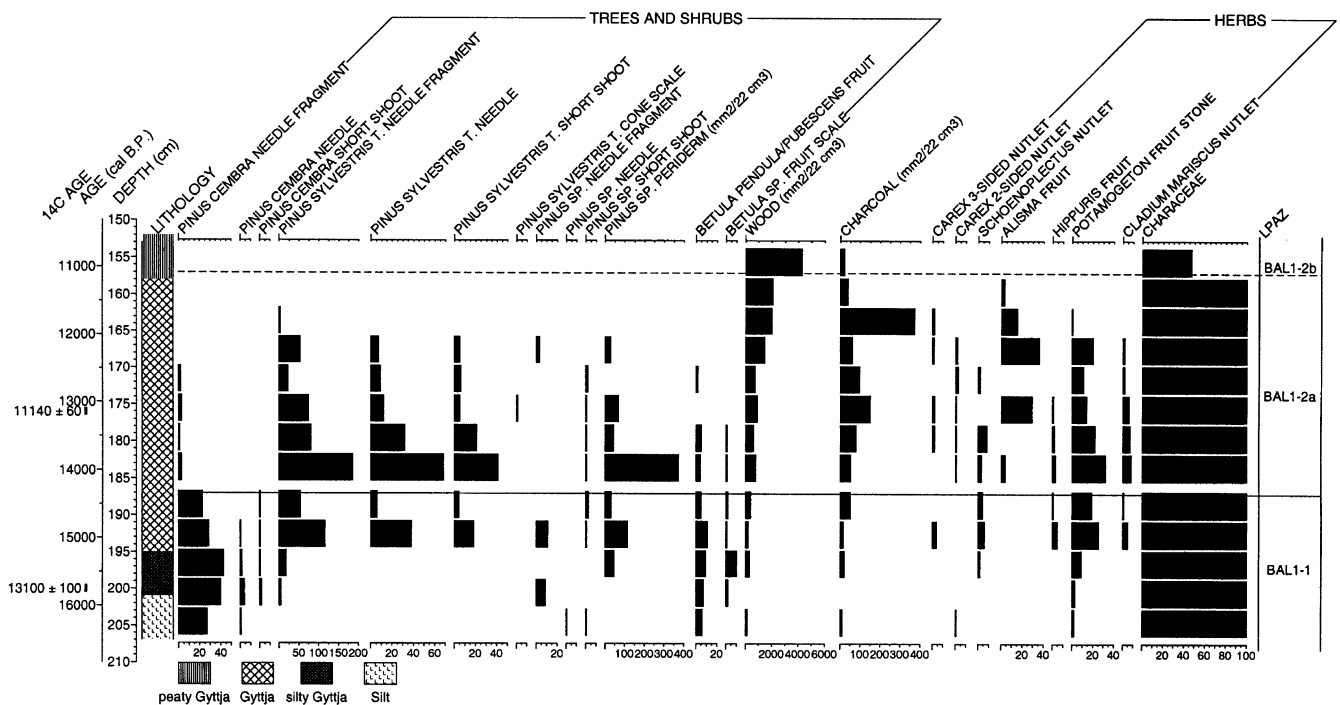


Fig. 5 Plant-macrofossil concentrations of core 1, BAL1, findings per 22 cm³ (selected taxa). T. = type, LPAZ = local pollen assemblage zones, dashed line = statistically non-significant zone limit. Analyst: S. Hofstetter

the lowest sample, appear in the subsequent samples, and increase around 15000 cal B.P. They reach their highest values at the beginning of the second zone (BAL1-2, 14000 cal B.P.). From ca. 12000 cal B.P. the overall macrofossil concentrations decrease, reaching very low values in the last two samples. In the plant-macrofossil stratigraphy of BAL2 (Fig. 7) total macrofossil concentration was very low throughout the record. Nevertheless, an older phase rich in conifer remains (*P. cembra* and *P. sylvestris* type) until the beginning of BAL2-2b (10600 cal B.P.) can be separated from a subsequent phase with the predominance of periderm of deciduous arboreal taxa. It's worth noting that a needle fragment of *Abies alba* could be identified at a depth of 140 cm (ca. 9000 cal B.P.).

Charcoal stratigraphy

The results of the microscopic charcoal stratigraphy of BAL1 and BAL2 are presented together with the pollen percentages (Figs. 4 and 6). In BAL1 two charcoal peaks occur, the older is dated at ca. 14750 cal B.P. and the younger at ca. 12250 cal B.P. However, the overall microscopic charcoal influx is low throughout core BAL1. On the contrary, in BAL2 it is markedly higher, especially during the middle part of the record. Influx begins to increase at about 3500 cal B.P., reaches a huge peak at around 2500 cal B.P. and remains high until 1400 cal B.P. Around 2500 cal B.P. macroscopic charcoal particles (Figs. 5 and 7) also reach high values. However, the overall pattern of macroscopic charcoal differs substantially from the microscopic one. Highest values of macroscopic charcoal concentra-

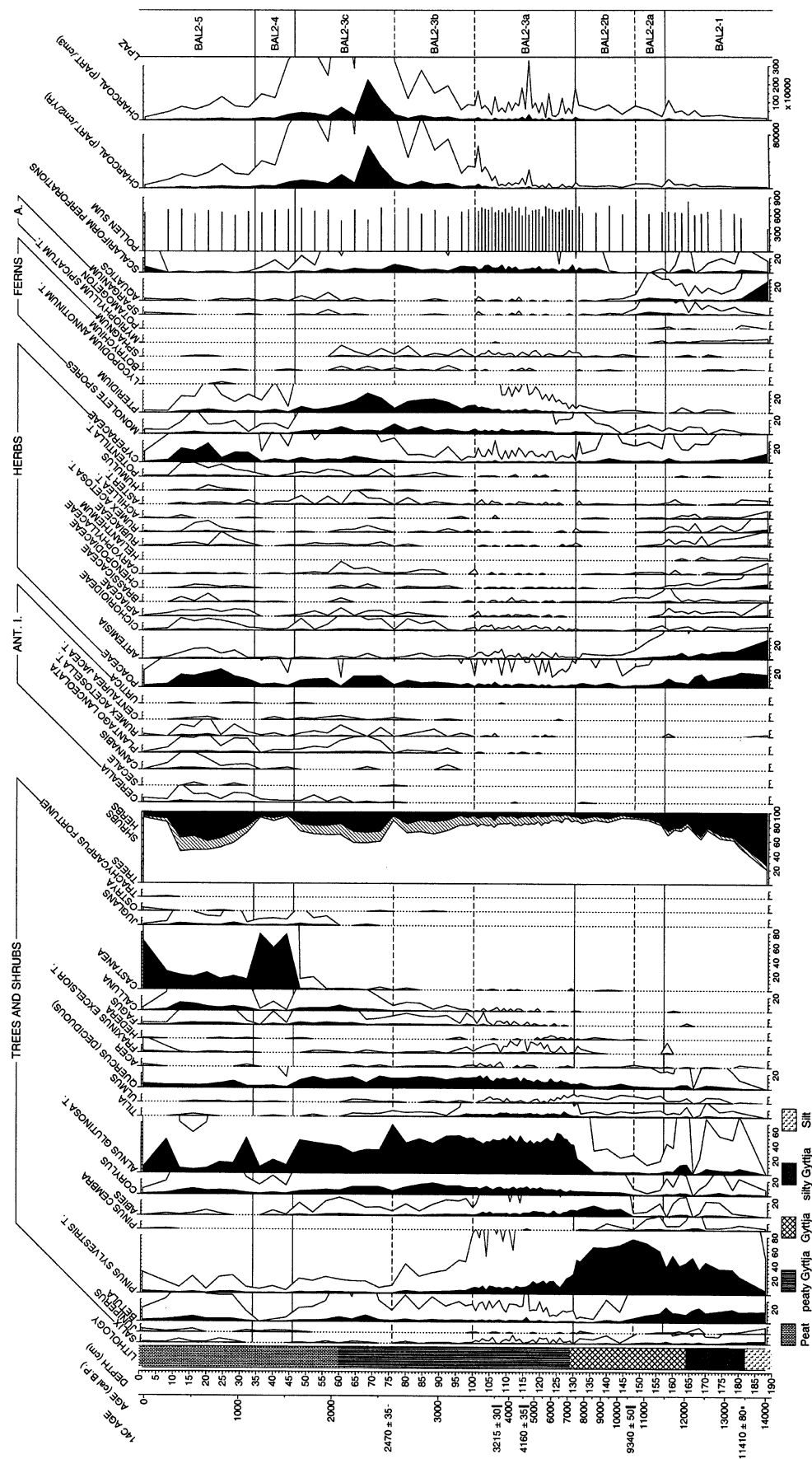
tions were reached at 12000 cal B.P. in BAL1 and at around 6000 cal B.P. in BAL2.

Discussion

Vegetation history, fire history and human impact at the study site

Pollen data of BAL1 (Fig. 4) suggest that at 16500 cal B.P. the landscape was open, with various shrubs and herbs. However, numerous *Pinus cembra* needles and *Betula* fruits (Fig. 5) indicate that afforestation had already started, with Swiss stone-pine and birch growing near the site. At about 16000 cal B.P. *P. sylvestris* type (*P. sylvestris* and *P. mugo*) appeared and became dominant at ca. 14000 cal B.P. Subsequently, it formed a forest together with *Betula*, whereas *P. cembra* was not important anymore. The pollen results from BAL2 show that vegetation during the early Holocene (Fig. 6) was still dominated by *P. sylvestris* type. It only decreased after 10600 cal B.P., when *Corylus* shrubs and *Abies* trees expanded. At that time *Ulmus*, *Quercus*, and *Acer* were also present. *Tilia* and *Fraxinus* became more important only around 8000 cal B.P., when *P. sylvestris* type finally declined and *Alnus glutinosa* became dominant. At about the same time the disappearance of aquatic plant macrofossils (e.g., *Potamogeton*, *Alisma*, Characeae, Figs. 4–7), together with the formation of peat, unambiguously documents the conversion of the former lake into a mire. The mixed stands of *Abies* and thermophilous trees were heavily disturbed at ca. 4000 cal B.P. (2050 B.C.) and destroyed at 3000 cal B.P. (1050 B.C.). This process was

Fig. 6 Pollen-percentage diagram of core 2, BAL2 (selected taxa). Exaggeration $\times 10$. T. = pollen type. Ant. I. = Anthropogenic indicators. A. = Aquatics. LPAZ = local pollen assemblage zones, dashed line = statistically non-significant zone limit. Analysts: S. Hofstetter, W. Tinner, V. Valsecchi



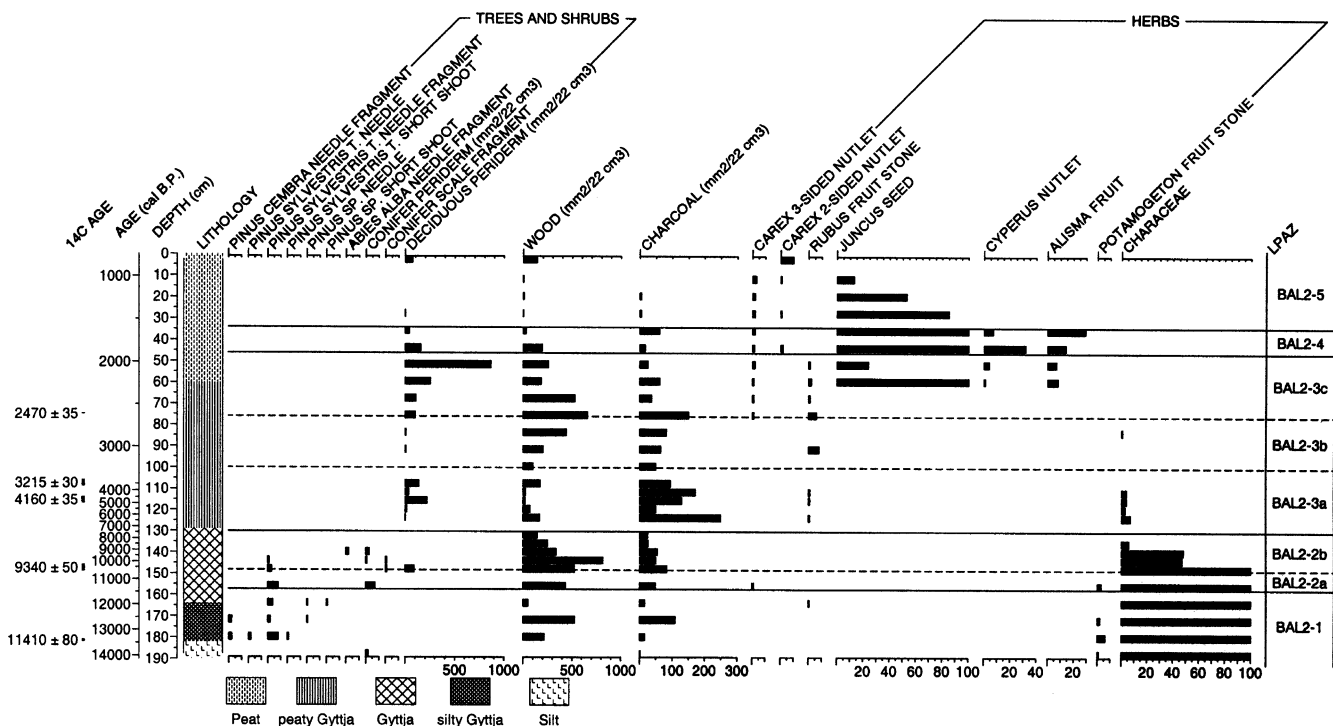


Fig. 7 Plant-macrofossil concentrations of core 2, BAL2, findings per 22 cm³ (selected taxa). T. = type. LPAZ = local pollen assemblage zones, dashed line = statistically non-significant zone limit. Analyst: S. Hofstetter

accompanied by the expansion of taxa indicative of human impact (*Plantago lanceolata*, *Cerealia*, *Rumex acetosella* t.) and disturbance (*Pteridium aquilinum*, monolete spores, and *Calluna vulgaris*). The increase of NAP percentages indicates that the landscape was rather open (tree pollen minimum <60%) between 3000 and 1500 cal B.P. (1050 B.C.–A.D. 450). After 1500 cal B.P. (A.D. 450) the surroundings were densely forested by *Castanea sativa*, with reduced cover between 1000 and ca. 100 cal B.P. (A.D. 950–1850).

Low microscopic charcoal influx suggests that regional forest-fire activity was low during the Lateglacial and early Holocene. However, some local fires must have occurred, as indicated by macroscopic charcoal particles (Fig. 5). A prominent peak in local fire activity was reached at about 6000 cal B.P. (Fig. 7). The regional relevance of fire increased for a first time around 5000 cal B.P., and after 3500 cal B.P. they were wide-spread. It is likely that they contributed to marked vegetation changes, such as the disruption of forests (NAP increase) and the expansion of *Pteridium aquilinum* (Tinner et al. 1999). Strong and frequent fires occurred around 2500 cal B.P., both at regional and at local scales. Finally, microscopic and macroscopic charcoal concentrations decreased and remained low after 1400 cal B.P.

First sporadic pollen of *Cerealia*, *Plantago lanceolata*, and *Urtica* occur during the Neolithic (5500–2200 B.C., Hochuli et al. 1998; Müller et al. 1999). It is likely, that human impact started at ca. 7000–5000 cal B.P. (5050–3050 B.C.). Slightly rising non-arboreal pollen percentages (e.g. Cichorioideae, *Artemisia*) and decreasing values of ar-

boreal taxa suggest first weak forest clearances. Increased local fire presence at around 6000 cal B.P. (4050 B.C.) could have resulted from early human slash-and-burn activities next to the study site. During the Bronze Age (2200–800 B.C., Hochuli et al. 1998; Müller et al. 1999), pollen data indicate that cultural activities such as pasturing became regionally more frequent. At the latest about 3000 cal B.P. (1050 B.C.) the landscape and vegetation became intensively used by people. Human activities further increased during the Iron Age (800–15 B.C., Hochuli et al. 1998; Müller et al. 1999), when huge microscopic charcoal concentrations as well as the collapse of many tree taxa indicate massive forest clearances. When *Castanea sativa* expanded after 2000 cal B.P., the original vegetation had definitively vanished.

The scale problem

Recent studies demonstrate that at small-scale sites a rather substantial proportion of total pollen is derived from regional sources (e.g., Sugita 1994; Calcote 1995; Jackson and Kearsley 1998; Parshall and Calcote 2001). Following these results, the relevant pollen source area of the mire at Balladrum is about 200–300 m, but only 30–45% of total pollen should come from within these distances. Nevertheless, small sedimentary basins are able to record local vegetation patterns, since it is assumed that 30–45% of the pollen load is sufficient to detect local changes when background pollen is consistent. It has been demonstrated that larger basin radii reduce the site-to-site variations of pollen loading and pollen proportion (Sugita 1994), so medium

to large basins (radius about 250–750 m) are thought to record the spatial distribution pattern of vegetation on more regional scales. Several studies (e.g., Odgaard 1992; Tinner et al. 1999) found significant correlations between pollen and microscopic charcoal. On the basis of these correlations it has been suggested that microscopic charcoal and pollen might have comparable source areas (Tinner and Hu 2003).

Common features with respect to previous results

Similar vegetation and fire histories were presented by all currently available medium to large-scale study sites in the lowlands of the Insubrian region, for instance at Lago di Ganna, 10 ha (Schneider and Tobolski 1985), Lago di Origlio, 8 ha (Tinner et al. 1999), Lago di Muzzano, 22 ha (Gobet et al. 2000), Lago del Segrino, 38 ha (Gobet et al. 2000), Lago di Lugano, 4890 ha (Wick 1989), and Lago di Annone, 550 ha (Wick Olatunbosi 1996). After the last ice-age, *Pinus sylvestris* type and *Betula* were the most important taxa during afforestation in the Insubrian Southern Alps. *P. cembra* was only important at Lago di Ganna (Schneider and Tobolski 1985) and Lago di Origlio (Tinner et al. 1999). Lateglacial forests were then successively replaced by temperate continental forests and shrublands. In the lowlands of the region *Abies alba* occurred at least since about 9400 cal B.P. Fire frequencies were low during the Lateglacial and early Holocene. During the Neolithic and Bronze Age *A. alba* and other arboreal taxa (e.g. *Tilia*, *Ulmus*, *Acer*, and *Fraxinus*) declined or disappeared completely. Since the fire records are significantly correlated with several declines of these taxa, it has been suggested that fire disturbance drove local extinctions of fire-sensitive taxa (Tinner and Conedera 1995; Tinner et al. 1999; Tinner et al. 2000). Forest clearances, changes in species composition, and fire frequencies reached their regional apex at 2600–2400 cal B.P. (650–450 B.C., i.e. during Iron Age). Further alterations happened at about 2000–1800 cal B.P., when *Castanea sativa* was favoured for economic purposes in the entire area of southern Switzerland (Conedera et al. 2004a). Pollen- and plant-macrofossil-inferred vegetation history at Ballardrum fits well with these previous reconstructions from large-scale sites. We can confirm the prominent role of fire in driving vegetation changes such as the disappearance of species (e.g. *Abies alba*) at a more local scale. Human impact seems somewhat reduced if compared with previous studies, but this may be explained by unfavourable local conditions for agriculture. According to early archaeological investigations, a Celtic settlement was situated on the top of the hill of Ballardrum (Crivelli 1945). This would explain the rather strong human signal in our record around 2500 cal B.P. (550 B.C.).

Differences to other sites and their indications

At Ballardrum *Alnus glutinosa* type is represented with extraordinarily high pollen percentages after 7000 cal

B.P., when the lake was converted into a mire. Conversely, other temperate taxa such as *Ulmus*, *Tilia*, *Fraxinus*, *Acer* or *Abies alba* seem to be underrepresented. These differences likely result from the small size of the basin and the reduced source area of pollen. With the filling-in of the lake into a mire, species needing wet conditions and growing next to the basins, such as *Alnus glutinosa*, were locally over-represented. However, other special local signals and surprising deviations from regional vegetation history cannot be fully explained only by size differences.

Pinus cembra (L.)

During the full glacial *P. cembra* forests probably grew near the southern border of the Alps (Lang 1994). The early presence of the Swiss stone pine was characteristic for the lateglacial afforestation in the Insubrian Southern Alps. It is assumed that the species played a major role in the modern montane belt (Landolt 2003), 600–1000 m a.s.l. (e.g. Zoller and Kleiber 1971; Wick Olatunbosi 1996). *P. cembra* forests also occurred at different sites in the lowlands. Zoller (1960) found a maximum of 9% *P. cembra* pollen at Lago di Origlio (416 m a.s.l.) in the Lateglacial. Better-dated modern palynological studies at the same lake (Tinner et al. 1999) revealed values up to 35%, documenting the importance of *P. cembra* between 16200 and 14700 cal B.P. At Lago di Ganna (452 m a.s.l.) *P. cembra* was important between ca. 16000 and 14000 cal B.P. (Schneider and Tobolski 1985). Pollen results suggest the mixed presence of *P. sylvestris* and *P. cembra*, but macrofossil results document an early period with *P. cembra* in which *P. sylvestris* was absent (Schneider and Tobolski 1985). However, in this early study the macrofossil-inferred *P. cembra* period was not dated by radiocarbon analyses. In the small mire at Ballardrum rather high values of Swiss stone-pine pollen are found shortly after the beginning of the record (ca. 16500 cal B.P., Fig. 4), percentage values show a peak of 24% at ca. 15000 cal B.P. Pollen results would suggest that *P. sylvestris* t. (including *P. mugo*) was growing together with *P. cembra* during this early period. However, in good biostratigraphical agreement with the Lago di Ganna results *P. cembra* was likely growing in pure stands before 16000 cal B.P. and was more important than *P. sylvestris* type until ca. 15000 cal B.P. (Fig. 5).

Not all lowland sites in the Insubrian region show such a *P. cembra* period. For example at Lago di Annone (226 m a.s.l.) and at Lago del Segrino (374 m a.s.l.) only very low pollen percentages of Swiss stone-pine were detected during the entire Lateglacial (Wick Olatunbosi 1996). *P. sylvestris* t. was predominant from the beginning of afforestation, and it seems that *P. cembra* was not competitive there. These differences in afforestation processes have not been explained heretofore. Since the area is rather small (the lakes Annone and Segrino are only 30 km distant from Ganna, Origlio, and Ballardrum) and *P. cembra* has a very effective dispersal mechanism (*Nucifraga caryo-catactes*,

Nutcrackers, up to 15 km per transport flight, Nilsson 1985), migrational effects can be excluded. The spatial differences might therefore be related to differences in environmental conditions. Today *P. cembra* shows ecological preferences different from those of *P. sylvestris* and *P. mugo*. To be competitive *P. cembra* needs cool and continental conditions, and it is not present in forests with mean annual air temperatures above about 3.5 °C (Ellenberg et al. 1992). With low moisture availability it is less competitive than *P. sylvestris* and *P. mugo* (Landolt 1977). In Siberia the distribution of *P. sibirica*, a very close relative of *P. cembra* (Gugerli et al. 2001), is related to moisture availability, with *P. sibirica* growing on more humid and *P. sylvestris* on drier slopes (Walter 1974). The absence or irrelevance of *P. cembra* in the calcareous areas of Insubria could be explainable by lower overall soil-moisture availability. Similar effects are documented for other species. For instance, at its northern temperature limit drought-adapted *Quercus pubescens* is competitive only in calcareous areas (Ozenda 1988; Steiger 1994; Ellenberg 1996), where ecological conditions are drier (Reisigl 1996). Additionally, recent observations (Carraro unpubl.) suggest that, in contrast to *P. mugo*, *P. cembra* is hardly able to grow on calcareous raw soils. Beside substrate effects, the sites of southern Switzerland may have benefited from orographic precipitation effects, as the region around the Lago Maggiore has higher orographic precipitation compared to adjacent areas of Insubria (Spinedi and Isotta 2004).

Abies alba (Mill.)

After 13500 cal B.P. pollen of *A. alba* is regularly present in the sediments of sites situated in the western part of the Insubrian Alps, possibly suggesting that the species occurred in this region already during the Lateglacial (Zoller 1964; Schneider 1978; Wick Olatunbosi 1996). On the basis of such early pollen findings, Schneider (1978) proposed that *A. alba* survived the last stadial at some favoured sites in the region of Ticino. However, until now the regular presence of pollen during the Lateglacial was only documented for high-altitudinal sites (e.g. at Suossa, 1700 m a.s.l., ca. 13500 cal B.P., and at Bedrina, 1235 m a.s.l., 12000–11500 cal B.P.; Zoller 1960; Zoller and Kleiber 1971; Küttel 1977). It is rather unlikely that these early finds at the high-altitudinal sites were only caused by long-distance transport of *A. alba* pollen during the Lateglacial, since Bedrina was certainly below treeline since at latest 14000–13500 cal B.P. (Allerød) and Suossa near treeline during the Allerød or just above treeline during the Younger Dryas (Welten 1982a,b; Tobolski and Ammann 2000; Gobet 2004). At all investigated lowland sites, the empirical limit (probably indicating isolated local stands, see Lang 1994) of *Abies* seems delayed: at ca. 10850 cal B.P. at Lago di Ganna (452 m a.s.l.) and at ca. 10500 cal B.P. at Lago di Origgio (416 m a.s.l.). The mass expansion (rational limit) occurred later, at about 9400–9000 cal B.P. (e.g., Schneider and Tobolski 1985; Wick Olatunbosi 1989; Tinner et al. 1999; Gobet et

al. 2000). In our new pollen record of the mire at Ballardrum the empirical limit of *A. alba* is dated to ca. 13000 cal B.P. in BAL1 and BAL2 (Figs. 4 and 6), whereas the mass expansion (rational limit) can be set at 10600 cal B.P. in BAL2 (Fig. 6). The empirical limit is therefore dated ca. 3000 years earlier and the rational limit about 1000 years earlier than at other study sites at comparable altitudes. One possible reason for this discrepancy might be the favourable local microhabitat. The species has high moisture requirements (Ellenberg 1996). It is conceivable that during dry phases of the Lateglacial and the early Holocene the hummocky landscape around Ballardrum provided microhabitats with enough moisture supply, especially in troughs such as the one around the Ballardrum mire. This explanation is sustained by the early high-altitudinal findings (e.g., empirical pollen limit of *Abies* at Bedrina and Suossa at 13000–12000 cal B.P.), because due to orographic effects it is likely that moisture availability was less limited with increasing altitude. However, due to the low amounts of pollen of *A. alba* at all Insubrian sites before ca. 11000 cal B.P., we cannot completely exclude that these early finds were caused by long-distance transport from the Apennines or further south, though this explanation seems rather unlikely for Ballardrum considering that the lowland site was situated in forested environments since at latest 16000 cal B.P. .

Castanea sativa (Mill.)

Conventionally it is assumed that the sweet chestnut was introduced into the Insubrian Southern Alps by the Romans about 2000 years ago (Zoller 1960; Schneider and Tobolski 1985; Wick Olatunbosi 1996; Tinner et al. 1999; Gobet et al. 2000). However, Zoller (1960) did not exclude an earlier presence, although isolated findings of *Castanea* pollen grains in sediments of pre-Roman times at Lago di Origgio and Bedrina were attributed to contamination. In fact these early findings could not be confirmed by subsequent re-analyses at Lago di Origgio and nearby Lago di Muzzano (Tinner et al. 1999; Gobet et al. 2000). However, several investigations emphasise that *C. sativa* most likely survived the last Ice Age in Italy and probably even at sheltered sites in northern Italy (Huntley and Birks 1983; Cruise 1990; Emmert-Straubinger 1991; Kelly and Huntley 1991; Paganelli and Miola 1991; Birks and Line 1993; Kaltenrieder et al. 2004). Some authors therefore consider the species as a natural component of forests in northern Italy and neighbouring areas (Mayer 1984; Paganelli 1996). The mass expansion of *Castanea* (rational limit) was synchronous in the Ballardrum record (Fig. 6) and the other sites of the region of southern Switzerland (approx. 1800–1600 cal B.P.). This is in agreement with the conventional opinion that sweet chestnut has been systematically cultivated in the area since Roman times (Conedera et al. 2004a). However, in contrast to all modern studies from the region, in the Ballardrum record *Castanea* pollen grains are found sporadically throughout the Holocene since about 9000 cal B.P., i.e., before the first occurrence of anthropogenic indicators. Since the

investigated mire is very small and even today under an almost closed canopy (Fig. 2), it is rather unlikely that the recovered grains could have resulted from distant sources. Although the small pollen grains of the sweet chestnut can be transported for long distances (Peeters and Zoller 1988), it is more likely that the grains originated from local trees in the case that downward pollen contamination is not a factor. In fact, we cannot exclude small down-core pollen movements in our compacted stratigraphy. Nevertheless, small-scale sites such as Balladrum can record local singularities of vegetation and are thus ideal to detect the presence of rare individuals. It is conceivable that single and rare *Castanea*-trees could have grown around Balladrum and that their pollen was caught in the small-scale basin. In agreement, Krebs et al. (2004) hypothesised that in southern Europe scattered favourable microsites existed for *C. sativa*, even in macro-areas generally thought to be unsuitable.

If sweet chestnut was present in the Insubrian Southern Alps during the pre-Roman Holocene, it did not have any stand-forming capacity. This would explain why at large-scale sites its pollen signal was not recorded. Natural *C. sativa* stands effectively occurred in southern Europe and the Caucasus, and their pollen imprint reached higher and uninterrupted values (Krebs et al. 2004). Since we cannot exclude contamination, further studies from small-scale sites are needed to prove the presence of *C. sativa* throughout the Holocene. Anthracological studies may be especially helpful to address this question, since they can unambiguously prove the former presence of tree species (Berli et al. 1994).

The advantage of considering varying basin sizes

Our comparison shows that the vegetation history of the small-scale mire at Balladrum partly differs substantially from one at large-scale study-sites in the Insubrian region, which recorded more homogenous vegetation histories. This difference is probably a result of different sizes of the sites and thereby the different varying pollen-source areas (e.g., Jacobson and Bradshaw 1981; Sugita 1994; Calcote 1995; Lynch 1996; Jackson and Kearsley 1998; Parshall and Calcote 2001). Our new study corroborates previous studies suggesting that only by investigating small-scale sites it is possible to detect rare species or species producing little or poorly dispersed pollen (e.g., Jackson and Kearsley 1998). Conversely, medium-sized and large sites can integrate different vegetation patches and therefore be used to detect large-scale patterns such as, e.g., vegetation dynamics in response to climatic change. In this sense, considering small sites alone could lead to many noisy and patchy local patterns that would be difficult to interpret. However, our study shows that an approach comparing sites of varying sizes can improve the reconstruction of vegetation history, especially if macrofossil analysis is included to further increase spatial resolution.

The natural potential vegetation

Natural plant communities are hardly recognizable anymore in the Insubrian southern Alps (Ozenda 1988; Hegg et al. 1993; Steiger 1994). Tinner et al. (1999) proposed that the natural vegetation of the Insubrian lowlands would be characterized by mixed forests of *Abies alba* and the deciduous trees *Tilia* (*T. cordata*, *T. platyphyllos*), *Quercus* (*Q. petraea*, *Q. pubescens*), *Alnus glutinosa*, *Fagus sylvatica*, *Fraxinus excelsior*, and *Ulmus* sp. Evergreen broad-leaved and submediterranean species would regularly occur in these forests. We suggest that in the region around the investigated mire the same species would be important if human impact would decrease or cease. With our new results, we corroborate the suggestion of Tinner et al. (1999) that also *Castanea sativa* would be present as single trees or small tree stands. However, the frequency of the different tree species would vary according to local environmental conditions. Due to the particular setting of the topography at Balladrum (steep stony slopes), *Abies alba* would be locally less important than at sites elsewhere in the Insubrian southern Alps. Similarly, other trees, such as *Tilia*, *Quercus*, *Fraxinus*, *Ulmus*, *Fagus*, and *Acer*, would be less frequent. In return, due to the frequent small wetlands, *Alnus glutinosa* would be more wide-spread. As climatic conditions around the investigated mire are extremely mild, probably laurophyllous species, such as *Laurus nobilis*, *Prunus laurocerasus*, and *Trachycarpus fortunei*, would be favoured.

Conclusions

The investigated small-scale mire records patterns that differ from those of nearby but considerably larger sites. This finding can be explained by adopting well-established models, showing that the pollen source area depends on the basin size of the studied site. We therefore confirm that the spatial resolution of the palaeo-record can be significantly improved by considering small-scale sites and also by investigating macrofossil records. Despite interesting differences for important taxa, we confirm the general traits of regional vegetation and fire history as reconstructed by previous pollen, macrofossil, and charcoal studies from medium to large-scale sites. This implies that in the Insubrian region similar long-term vegetation dynamics occurred at different scales, from regionally (e.g., Lago di Lugano, with several kilometres of pollen catchment) to locally (Balladrum, with several decametres of pollen catchment). As documented by this study the most important factors that triggered vegetation changes during the Holocene were fire and human impact. Finally we show that the previously elaborated concepts to assess the natural potential vegetation (Tinner et al. 1999) can be transferred to small scales, if local environmental conditions are taken into account.

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References

- Bennett KD (1996) Determination of the numbers of zones in a biostratigraphical sequence. *New Phytol* 132:155–170
- Berli S, Cherubini P, Schoch W (1994) Rekonstruktion von Bestandesfluktuationen, Bodenmächtigkeit und Feuergeschichte über 7000 Jahre BP mittels Holzkohle-Analysen. *Botan Helvet* 104:17–30
- Beug H-J (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, München
- Birks HH (2001) Plant macrofossils. In: Smol JP, Birks HJB, Last WM (eds) *Tracking environmental change using lake sediments*. Kluwer Dordrecht 49–71
- Birks HH (2003) The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. *Quatern Sci Rev* 22:453–473
- Birks HH, Birks HJB (2000) Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeogr* 27:31–35
- Birks HJB, Gordon AD (1985) *Numerical methods in Quaternary pollen analysis*. Academic Press, London
- Birks HJB, Line JM (1993) Glacial refugia of European trees—a matter of chance? *Veg Hist Archaeobot* 196:283–291
- Broström A, Gaillard M-J, Ihse M, Odgaard B (1998) Pollen-landscape relationship in modern analogues of ancient cultural landscapes in southern Sweden - a first step towards quantification of vegetation openness in the past. *Veg Hist Archaeobot* 7:189–201
- Calcote R (1995) Pollen source area and pollen productivity: evidence from forest hollows. *J Ecol* 83:591–602
- Carraro G, Gianoni P, Mossi GR, Klötzli F, Walther G-R (1999) Observed changes in vegetation in relation to climate warming. Vdf Hochschulverlag ETH, Zürich
- Clark JS (1995) Particle-size evidence for source areas of charcoal accumulation in Late Holocene sediments of Eastern North American Lakes. *Quatern Res* 43:80–89
- Clark JS, Merkt J, Müller H (1989) Post-glacial fire, vegetation and human history on the northern alpine forelands, south-western Germany. *J Ecol* 77:897–925
- Conedera M, Hofmann C, Tinner W (1999) Vegetation shift and laurophyllisation: the possible role of forest fires. In: Kloetzli F, Walther G-R (eds) *Recent shifts in vegetation boundaries of deciduous forests*. Birkhäuser, Basel, 1–11
- Conedera M, Stanga P, Lischer C, Stoeckli V (2000) Competition and dynamics in abandoned chestnut orchards in southern Switzerland. *Ecologia Mediterranea* 26:101–112
- Conedera M, Stanga P, Oester B, Bachmann P (2001) Different post-culture dynamics in abandoned chestnut orchards and coppices. *For Snow and Lands Res* 76:487–492
- Conedera M, Krebs P, Tinner W, Pradella M, Torriani D (2004a). The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale. *Veg Hist Archaeobot* 13:161–179
- Conedera M, Stanga P, Oester B, Bachmann P (2004b) Natural dynamics of abandoned chestnut stands in southern Switzerland. In: Mazzoleni S, Pasquale G di, Mulligan M, Martino P di, Rego F (eds) *Recent dynamics of the mediterranean vegetation and landscape*. Wiley, West Sussex, 237–247
- Crivelli A (1945) Una sensazionale scoperta ad Ascona *Rivista storica ticinese*. 8:1043–1044
- Cruise GM (1990) Pollen stratigraphy of two Holocene peat sites in the Ligurian Apennines, Northern Italy. *Rev Palaeobot Palynol* 63:299–313
- Ehrensberger K (1984) *Vegetationskundliche Untersuchungen im Gebiet Losone-Arcegnò*. Diploma thesis University of Bern, Bern
- Ellenberg H (1996) *Vegetation Mitteleuropas mit den Alpen*, 5th edn. Ulmer, Stuttgart
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1992) Indicator values of plants in Central Europe. *Scripta Geobotanica*. Goltze, Göttingen
- Emmert-Straubinger E (1991) *Die Interglazialflora von Pianico (Prov. Bergamo, Italien)*. Palaeovegetational development in Europe and regions relevant to its palaeofloristic evolution. In: Kovar-Ederl J, (ed) *Proceedings of Pan-European Palaeobotanical Conference*, Museum of Natural History, Department of Geology and Palaeontology, Vienna, 15–18
- Finsinger W, Tinner W (2005) Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. *The Holocene* 15(2):293–297
- Frehner M, Wasser B, Schwittr R (2005) Nachhaltigkeit im Schutzwald und Erfolgskontrolle - Wegleitung für Pflegemaßnahmen in Wäldern mit Schutzfunktion. BUWAL, Bern
- Gianoni P, Carraro G, Kloetzli F (1988) Thermophile, an laurophyllen Pflanzenarten reiche Waldgesellschaften im hyperinsubrischen Seengebiete des Tessins. *Bericht des Geobotanischen Institutes der ETH Stiftung Rübel* 54:164–180
- Gobet E (2004) *Landschafts- und Vegetationsdynamik der letzten 12'000 Jahre im Oberengadin*. PhD Thesis, University of Bern, Bern
- Gobet E, Tinner W, Hubschmied P, Jansen I, Wehrli M, Ammann B, Wick L (2000) Influence of human impact and bedrock differences on the vegetational history of the Insubrian Southern Alps. *Veg Hist Archaeobot* 9:175–178
- Grimm EC (1992) *Tilia 2.0 and Tilia graph 1.18*. Illinois State Museum, Research and Collection Center, Springfield
- Grund K, Conedera M, Schröder H, Walther G-R (2004) The role of fire in the invasion process of evergreen broad-leaved species. *Basic and Applied Ecology*, in press
- Gugerli F, Senn J, Anzidei M, Madaghiale A, Buchler U, Sperisen C, Vendramin GG (2001) Chloroplast microsatellites and mitochondrial nad1 intron 2 sequences indicate congruent phylogenetic relationship among Swiss stone pine (*Pinus cembra*), Siberian stone pine (*Pinus sibirica*), and Siberian dwarf pine (*Pinus pumila*). *Mol Ecol* 10:1489–1497
- Hantke R (1983) *Eiszeitalter, die jüngste Erdgeschichte der Schweiz und ihrer Nachbargebiete* 3. Ott, Thun
- Hegg O, Beguin C, Zoller H (1993) *Atlas schutzwürdiger Vegetationstypen der Schweiz*. BUWAL, Bern
- Hochuli S, Niffeler U, Rychner V (1998) *Die Schweiz vom Paläolithikum bis zum frühen Mittelalter - Bronzezeit*. Schweizerische Gesellschaft für Ur- und Frühgeschichte, Basel
- Huntley B, Birks HJB (1983) *An atlas of past and present pollen maps for Europe: 0–13 000 years ago*. Cambridge University Press, Cambridge
- Jackson ST, Kearsley FB (1998) Quantitative representation of local forest composition in forest-floor pollen assemblages. *J Ecol* 86:474–490
- Jacobson GL, Bradshaw RH (1981) The selection of sites for paleovegetational studies. *Quatern Res* 16:80–96
- Kaltenrieder P, Ammann B, Ravazzi C, Tinner W (2004) Long-term forest dynamics during the past 26000 years at Colli Euganei (near Padova, Italy). In: Uberti JL (ed) *11th International Palynological Congress, Granada, POLEN*. Servicio de Publicaciones Universidad de Cordoba, Cordoba, pp 601
- Kelly MG, Huntley B (1991) An 11 000-year record of vegetation and environment from Lago di Martignano, Latium, Italy. *J Quatern Sci* 6:209–224
- Kloetzli F, Walther G-R, Carraro G, Grundmann A (1996) Anlaufender Biomwandel in Insubrien. *Verhandlungen der Gesellschaft für Ökologie* 26:537–550
- Krebs P, Conedera M, Pradella M, Torriani D, Felber M, Tinner W (2004) Quaternary refugia of the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach. *Veg Hist Archaeobot* 13:145–160

- Küttel M (1977) Pollenanalytische und geochronologische Untersuchungen zur Piottino-Schwankung (Jüngere Dryas). *Boreas* 6:259–274
- Labhart TP (1995) *Geologie der Schweiz*. Ott, Thun
- Landolt E (1977) Ökologische Zeigerwerte zur Schweizer Flora. Veröffentlichung des Geobotanischen Institutes der ETH Stiftung Rübel, Zürich
- Landolt E (2003) *Unsere Alpenflora*. Egger, Frutigen
- Lang G (1994) *Quartäre Vegetationsgeschichte Europas*. Gustav Fischer, Jena Stuttgart, New York
- Lynch EA (1996) The ability of pollen from small lakes and ponds to sense fine-scale vegetation patterns in the Central Rocky Mountains, USA. *Rev Palaeobot Palynol* 94:197–210
- MacDonald GM, Larsen CPS, Szeicz JM, Moser KA (1991) The reconstruction of boreal forest fire history from lake sediments: a comparison of charcoal, pollen sedimentological and geochemical indices. *Quatern Sci Rev* 10:53–71
- Maggini L, Spinedi F (1996) Misurazioni meteorologiche al Parco botanico delle Isole di Brissago 1962–1995. *Bollettino della Società Ticinese di Scienze Naturali* 84:65–71
- Mayer H (1984) *Wälder Europas*. Gustav Fischer, Stuttgart
- Merkel J, Streif H (1970) Stechrohr-Bohrgeräte für limnische und marine Lockersedimente. *Geologisches Jahrbuch* 88:137–148
- Moore PD, Collinson ME, Webb JA (1991) *Pollen analysis*. 2nd edn. Blackwell Science, London
- Müller F, Kaenel G, Lüscher G (1999) Die Schweiz vom Paläolithikum bis zum frühen Mittelalter - Eisenzeit. Schweizerische Gesellschaft für Ur- und Frühgeschichte, Basel
- Nilsson SG (1985) Ecological and evolutionary interactions between reproduction of beech *Fagus sylvatica* and seed eating animals. *Oikos* 44:157–164
- Odgaard BV (1992) The fire history of Danish heathland areas as reflected by pollen and charred particles in lake sediments. *The Holocene* 2:218–226
- Ozenda P (1988) *Die Vegetation der Alpen im europäischen Gebirgsraum*. Gustav Fischer, Stuttgart New York
- Paganelli A (1996) A palynological study of forest vegetation in the Veneto-Po Plain. *Allionia, Bollettino di Dipartimento di Biologia Vegetale dell' Università di Torino* 34:189–218
- Paganelli A, Miola A (1991) Chestnut (*Castanea sativa* Mill.) as an indigenous species in northern Italy. *Il Quaternario* 4:99–106
- Parshall T, Calcote R (2001) Effect of pollen from regional vegetation on stand-scale forest reconstruction. *The Holocene* 11:81–87
- Peeters GA, Zoller H (1988) Long range transport of *Castanea sativa* pollen. *Grana* 27:203–207
- Reille M (1992) Pollen et Spores d'Europe et d'Afrique Du Nord. Laboratoire de botanique historique et palynologie, Marseille
- Schneider R (1978) Pollenanalytische Untersuchungen zur Vegetationsgeschichte am Südrand der Alpen zwischen Turin und Varese (Italien). *Botanische Jahrbücher zur Systematik und Pflanzengeschichte* 100:26–109
- Schneider R, Tobolski K (1985) Lago di Ganna - Lateglacial and Holocene Environments of a lake in the Southern Alps. *Dissertationes Botanicae* 87:229–271
- Schoch WH, Pawlik B, Schweingruber FH (1988) *Botanische Makroreste*. Haupt, Bern
- Spinedi F, Isotta F (2004) Il clima del Ticino. Dati, statistiche e società 4:5–39
- Steiger P (1994) *Wälder der Schweiz*. Ott, Thun
- Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13:615–621
- Struzkova D (2002) Cuticular Analysis - a method to distinguish the leaves of *Pinus sylvestris* L. (Scots Pine) from those of *Pinus mugo* Turra s.str. (Dwarf Mountain-pine). *Veg Hist Archaeobot* 11:241–246
- Stuiver M, Reimer PJ (1998) Extended ¹⁴C data base and revised Calib. 4.1.2, ¹⁴C age calibration program. *Radiocarbon* 35:215–230
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J Ecol* 82:881–897
- Sugita S, Gaillard M-J, Broström A (1999) Landscape openness and pollen records: a simulation approach. *The Holocene* 9:409–421
- Tinner W, Conedera M (1995) Indagini paleobotaniche sulla storia della vegetazione e degli incendi forestali durante l'Olocene al Lago di Origgio (Ticino meridionale). *Bollettino della Società Ticinese di Scienze Naturali* 83:91–106
- Tinner W, Conedera M, Ammann B, Gaeggeler HW, Gedye S, Jones R, Saegesser B (1998) Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. *The Holocene* 8:31–42
- Tinner W, Conedera M, Gobet E, Hubschmid P, Wehrli M, Ammann B (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10:527–536
- Tinner W, Hu FS (2003) Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13:499–505
- Tinner W, Hubschmid P, Wehrli M, Ammann B, Conedera M (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *J Ecol* 87:273–289
- Tobolski K (1992) *Pflanzliche Makroreste in Seesedimenten und Torf. Bestimmungsschlüssel zum Praktikum Paläoökologie Wintersemester 92/93*. University of Bern, Bern
- Walter H (1974) *Die Vegetation Osteuropas, Nord- und Zentralasiens*. Gustav Fischer, Stuttgart
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Whitlock C, Larsen C (2001) Charcoal as fire proxy. In: Smol JP, Birks HJB, Last WM (eds) *Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators*. Kluwer, Dordrecht, 75–97
- Wick L (1989) Pollenanalytische Untersuchungen zur spät- und postglazialen Vegetationsgeschichte am Luganersee (Südtessin, Schweiz). *Eclogae Geologicae Helvetiae* 82:265–276
- Wick Olatunbosi L, (1996) Spät- und postglaziale Vegetationsgeschichte in den Südalpen zwischen Comersee und Splügenpass (Norditalien). Thesis University of Bern, Bern
- Zoller H (1960) Die kulturbedingte Entwicklung der insubrischen Kastanienregion seit den Anfängen des Ackerbaus im Neolithikum. *Bericht des Geobotanischen Institutes der ETH Stiftung Rübel* 32:263–279
- Zoller H (1964) Zur postglazialen Ausbreitungsgeschichte der Weissstanne (*Abies alba* Mill.) in der Schweiz. *Schweizerische Zeitschrift für Forstwesen* 11:681–700
- Zoller H, Kleiber H (1971) Vegetationsgeschichtliche Untersuchungen in der montanen und subalpinen Stufe der Tessintäler. *Verhandlungen der Naturforschenden Gesellschaft Basel* 81:90–154